

## Consistent effects of consumer species loss across different habitats

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## CONSISTENT EFFECTS OF CONSUMER SPECIES LOSS ACROSS DIFFERENT HABITATS

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Abstract:	<p>Our knowledge of the effects of consumer species loss on ecosystem functioning is limited by a paucity of manipulative field studies, particularly those that incorporate inter-trophic effects. Further, given the ongoing transformation of natural habitats by anthropogenic activities, studies should assess the relative importance of biodiversity for ecosystem processes across different environmental contexts by including multiple habitat types. We tested the context-dependency of the effects of consumer species loss by conducting a 15-month field experiment in two habitats (mussel beds and rock pools) on a temperate rocky shore, focussing on the responses of algal assemblages following the single and combined removals of key gastropod grazers (<i>Patella vulgata</i>, <i>P. ulyssiponensis</i>, <i>Littorina littorea</i> and <i>Gibbula umbilicalis</i>). In both habitats, the removal of limpets resulted in a larger increase in macroalgal richness than that of either <i>L. littorea</i> or <i>G. umbilicalis</i>. Further, by the end of the study, macroalgal cover and richness were greater following the removal of multiple grazer species compared to single species removals. Despite substantial differences in physical properties and the structure of benthic assemblages between mussel beds and rock pools, the effects of grazer loss on macroalgal cover, richness, evenness and assemblage structure were remarkably consistent across both habitats. There was, however, a transient habitat-dependent effect of grazer removal on macroalgal assemblage structure that emerged after three months, which was replaced by non-interactive effects of grazer removal and habitat after 15 months. This study shows that the effects of the loss of key consumers may transcend large abiotic and biotic differences between habitats in rocky intertidal systems. While it is clear that consumer diversity is a primary driver of ecosystem functioning, determining its relative importance across multiple contexts is necessary to understand the consequences of consumer species loss against a background of environmental change.</p>

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2                               **ACROSS DIFFERENT HABITATS**

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16 **Abstract:**

17

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## Introduction

Global biodiversity loss continues to threaten the provision of ecosystem services and ultimately human wellbeing (Naeem et al. 2009, Hooper et al. 2012). Following more than two decades of intensive research, it is now accepted widely that declining biodiversity affects rates of ecosystem processes, such as resource capture and biomass production (Loreau et al. 2001, Cardinale et al. 2012, Gamfeldt et al. in press). In recognition of the complexity of biotic interactions within natural communities, an increasing number of biodiversity–ecosystem functioning studies have incorporated inter-trophic effects (Duffy et al. 2007). Despite this important move towards a multi-trophic perspective, our knowledge of the influence of consumer diversity loss on lower trophic levels is relatively incomplete (Duffy et al. 2007, Griffin et al. 2013). This is of particular concern, given that consumers generally have impacts that are disproportionate to their abundance and face a higher risk of extinction compared to producers (Duffy 2002).

Long-term field removal experiments are an effective means of characterising the effects of species loss within diverse natural assemblages (Díaz et al. 2003) and complement laboratory studies by revealing mechanisms that may not be manifested in smaller scale experiments conducted under more homogeneous conditions (Stachowicz et al. 2008). Further, as the ecological effects of biodiversity change are influenced by environmental context (Boyer et al. 2009, Crowe et al. 2011, Mrowicki and O'Connor in press), empirical studies that examine consumer diversity effects under a range of abiotic and biotic conditions (Griffin et al. 2009, O'Connor and Donohue 2013) will improve our ability to predict the consequences of species loss in the face of global environmental change involving multiple anthropogenic stressors (Harley et al. 2006).

66

67 Coastal ecosystems are exposed to a range of anthropogenic impacts, which can result in  
 68 rapid declines in biodiversity and dramatic transformation or loss of habitat (Airoidi and Beck  
 69 2007). For example, on temperate rocky shores, overexploitation and pollution, coupled with  
 70 the physiological and phenological responses of organisms to climate change, may lead to  
 71 reduced densities or extinctions of key grazer species in certain localities (Thompson et al.  
 72 2002, Mieszkowska et al. 2005). Additionally, intertidal biogenic habitats, such as macroalgal  
 73 and mussel beds on rocky substrata, have decreased in extent and structural complexity in  
 74 many regions in response to various factors including physical disturbance and compromised  
 75 water quality (Airoidi and Beck 2007). Changes in habitat complexity and heterogeneity alter  
 76 interspecific interactions and the degree of resource partitioning among consumers, and can  
 77 thus modify consumer diversity effects on resources (Hughes and Grabowski 2006, Griffin et  
 78 al. 2009). In combination, these processes have the potential to shift the dynamic balance  
 79 between producers and consumers and alter the functioning of coastal marine ecosystems  
 80 (Hawkins et al. 2009).

81

82 The aim of this study was to determine whether the ecological consequences of consumer  
 83 species loss vary with environmental context, in light of ongoing reductions in biodiversity  
 84 and habitat homogenisation in coastal ecosystems. We quantified changes in macroalgal  
 85 assemblages in response to individual and combined removals of common gastropod grazers,  
 86 *Patella vulgata*, *P. ulyssiponensis*, *Littorina littorea* and *Gibbula umbilicalis*, in two different  
 87 habitats on an exposed north-east Atlantic rocky shore. Patellid limpets are key grazers in  
 88 European rocky intertidal habitats, and although their presence or absence often dominates the  
 89 effects of grazer assemblages on algal communities on emergent rock and in rock pools  
 90 (Hawkins and Hartnoll 1983, O'Connor and Crowe 2005, Coleman et al. 2006, Griffin et al.

2010), the extent of their influence in other habitats, such as mussel beds, is less well known (O'Connor and Crowe 2008). Further, the relative roles of these grazer species may vary across different conditions, and the importance of changes in the richness versus identity of these species is likely to increase with environmental heterogeneity (Griffin et al. 2009). To examine the context-dependency of the roles of these key consumers, we performed simultaneous grazer removals in mussel beds (on emergent rock) and in rock pools. These two distinct habitats differ greatly with respect to the intensity and variability of a range of abiotic stressors such as desiccation potential, temperature and wave disturbance. Specifically, emergent rock habitats experience relatively greater fluctuations in abiotic variables, but conditions can be more spatially variable among rock pools (Metaxas and Scheibling 1993). At the same time, the physical structure afforded by either mussels or turf algae (e.g. *Corallina officinalis*) enables diverse, yet divergent, biotic assemblages to persist (Seed 1996, Kelaher 2002). Thus, owing to contrasting patterns of physical and biological heterogeneity in mussel beds versus rock pools, the relative effects of grazer removal may differ between these two habitats. Focussing on changes in macroalgal abundance, diversity and assemblage structure, we hypothesised that: (1) there are species-specific consumer identity effects, dominated by the influence of *Patella* spp. in both mussel beds and rock pools; (2) the effects of the combined removal of multiple grazer species will exceed the effects of removals of single species; and (3) these effects of grazer species loss will differ between rock pools and mussel beds and vary according to experimental duration.

## Materials and methods

### *Study site*



116 The experiment was conducted on an exposed rocky shore in Glashagh Bay, Fanad, Co.  
 117 Donegal, Ireland (55.265°N, 7.675°W). The shore was characterised by a large, gently sloping  
 118 granitic platform, covered by a mosaic of patches of barnacles and macroalgae, typical of  
 119 exposed shores in the region (O'Connor and Crowe 2008, Mrowicki et al. 2014). Beds of  
 120 mussels (*Mytilus* spp.) were distributed patchily along the shore above mid-tidal level (2.0–  
 121 2.5 m above Chart Datum). Numerous discrete rock pools of varying area and depth were  
 122 present throughout the intertidal zone. Macroalgal assemblages associated with mussels  
 123 consisted of extensive epibiotic turfs of coarse red algae (mostly *Gelidium* spp.) interspersed  
 124 with ephemeral red (e.g. *Porphyra umbilicalis*) and green (e.g. *Ulva intestinalis*) algae. Small  
 125 clumps of brown algae (e.g. *Fucus spiralis* and *F. serratus*) were also found in and around the  
 126 mussel beds. The rock pools were dominated by turfs of upright calcareous algae (*Corallina*  
 127 *officinalis*), which supported an array of macroalgal species including fine (e.g. *Polysiphonia*  
 128 *elongata* and *Ceramium rubrum*) and coarse (e.g. *Osmundea hybrida* and *Gelidium* spp.)  
 129 branched red algae, ephemeral (e.g. *U. compressa*) and perennial (e.g. *Codium tomentosum*)  
 130 green algae and brown canopy algae (e.g. *F. vesiculosus* and *Halidrys siliquosa*). Encrusting  
 131 coralline algae (*Lithothamnion* spp.) covered most of the remaining substratum. Thus, on this  
 132 shore, in addition to there being large differences in algal assemblage structure between the  
 133 two habitats, the diversity of algae was greater in rock pools compared to mussel beds (see  
 134 *Results*).

135

136 Grazing gastropods were common and widespread across the shore. The most conspicuous  
 137 species, which occurred in both mussel beds and rock pools, were the common and China  
 138 limpets (*Patella vulgata* and *P. ulyssiponensis*, respectively), common periwinkle (*Littorina*  
 139 *littorea*) and flat top shell (*Gibbula umbilicalis*). Although the two limpet species co-occurred  
 140 in both habitat types, particularly as newly settled juveniles in rock pools, *P. ulyssiponensis*

adults were dominant in rock pools (Firth and Crowe 2008), whereas *P. vulgata*, which tends to disperse out onto emergent rock, constituted the majority of limpets in mussel beds. Other gastropod species, including *L. saxatilis*, *L. obtusata* and *G. cineraria*, were also present in both habitats. Non-gastropod grazers such as chitons (e.g. *Acanthochitona crinita*) and amphipods (e.g. *Echinogammarus marinus*) were found on the shore at lower densities.

#### *Experimental design*

Our experiment involved the single and combined removal of three genera of gastropod grazer within each of the two habitat types (mussel beds and rock pools). We employed a ‘subtractive’ approach with no compensation for the reduction in biomass of particular species by increasing that of the remaining species. Unlike a substitutive design, whereby total grazer density would be equalised across treatments, such an approach avoids confounding changes in intraspecific interactions with changes in interspecific interactions among grazers (Byrnes and Stachowicz 2009). Further, instead of standardising species densities across habitat types, we opted to mimic actual densities specific to mussel beds and rock pools. Thus, we did not elicit potentially unsustainable experimental densities by exceeding natural densities in either habitat (Harley 2006) and we minimised transplant-induced stress or mortality of grazers, particularly limpets (Firth and Crowe 2010). Importantly, although our design did not allow the effects of grazer removal and habitat type to be separated from those of grazer density, incorporating (rather than eliminating) natural variability in species densities was intended to enhance the realism of our study (Diaz et al. 2003) with respect to this particular system.

Within each of the two habitats, 20 plots ( $35 \times 35$  cm) were located haphazardly around mid-tidal level across approximately 100 m of shoreline, with a minimum separation between any two plots of 1 m. Mussel bed plots were positioned on well-drained, approximately horizontal, substratum and incorporated  $50.8 \pm 2.2\%$  (mean  $\pm$  SE) mussel cover. Rock pool plots were situated in separate pools of relatively similar area (range  $0.5\text{--}5.0$  m<sup>2</sup>) and depth ( $< 15$  cm) and included  $46.5 \pm 4.2\%$  cover of *Corallina officinalis*. By incorporating, rather than controlling for, environmental heterogeneity such as inherent differences in habitat size (i.e. mussel patch extent and rock pool volume), we aimed to enhance the relevance of this study to variable natural systems.

Five grazer removal treatments were assigned randomly among the plots in each habitat type ( $n = 4$ ): one ‘non-removal’ treatment requiring the removal of no species; three ‘single-removal’ treatments involving the removal of either *Patella* spp. (*P. vulgata* and *P. ulyssiponensis*; hereafter *Patella*), *Littorina littorea* (hereafter *Littorina*) or *Gibbula umbilicalis* (hereafter *Gibbula*); and one ‘multi-removal’ treatment, in which all three grazer genera were removed. Owing to difficulties in the identification of *P. vulgata* and *P. ulyssiponensis*, particularly juveniles and small adults, without causing substantial disturbance, it was not possible to discriminate between limpet species. On rocky shores in Ireland, adults of these two species tend to be segregated so that *P. vulgata* is more common on emergent substrata than *P. ulyssiponensis*, which is more common in rock pools (Firth and Crowe 2010). Further, there is the potential for contrasting functional roles of different limpet species within the same habitat (Moore et al. 2007). Therefore, it is not possible here to separate the effects of *P. vulgata* and *P. ulyssiponensis* across mussel beds and rock pools. Instead, as both species are considered key grazers within their respective primary habitats (Hawkins and Hartnoll 1983, O’Connor and Crowe 2005), the removal of *Patella* should be

190 interpreted as the combined loss of putative strongly-interacting consumers in the case of both  
191 mussel beds and rock pools. While it is possible here to make inferences regarding the  
192 specific roles of *Littorina* and *Gibbula*, caution must be exercised when attributing the effects  
193 of *Patella* removal, and their context-dependency, to particular species.

194  
195 Experimental grazer abundances were derived from natural densities in mussel beds (*Patella*,  
196  $27.5 \pm 6.2 \text{ m}^{-2}$  [mean  $\pm$  SE;  $n = 25$ ]; *Littorina*,  $40.3 \pm 14.3 \text{ m}^{-2}$ ) and rock pools (*Patella*,  $201.6$   
197  $\pm 26.8 \text{ m}^{-2}$ ; *Littorina*,  $90.2 \pm 13.9 \text{ m}^{-2}$ ; *Gibbula*,  $9.6 \pm 2.9 \text{ m}^{-2}$ ), adjusted to account for the high  
198 proportion (~50%) of *Patella* juveniles (< 15 mm) encountered in both habitat types.

199 Although not encountered within the area sampled by preliminary surveys, *Gibbula* was  
200 present in mussel beds at low overall density, often in small aggregations adjacent to mussel  
201 patches (R. J. Mrowicki, pers. obs.). Thus, experimental abundances were as follows: 3  
202 *Patella*, 5 *Littorina* and 2 *Gibbula* in mussel bed plots; and 12 *Patella*, 11 *Littorina* and 2  
203 *Gibbula* in rock pool plots. In a few cases, *Littorina* and *Gibbula* populations were  
204 supplemented with additional individuals to meet target densities, although this was not  
205 necessary for *Patella*. Treatments were maintained using stainless steel mesh cages (35 ×  
206 35 cm area, 12 cm high) fixed to the substratum with stainless steel screws and washers. This  
207 method was found to be most effective means of manipulating densities of mobile grazers  
208 over extended time periods on this particular shore. The mesh size (0.9 mm wire diameter,  
209 4.17 mm aperture, 67% open area) of cages restricted the movement of the target grazer  
210 species while allowing access to smaller mobile consumers and leaving plots open to  
211 propagule supply.

212  
213 To enable the detection of cage effects on experimental assemblages, an additional four plots  
214 were established within each habitat and marked at opposite corners with stainless steel

screws, thus remaining open to ambient densities of mobile organisms. Although there is the potential for experimental artefacts to vary among treatments (Peterson and Black 1994, Benedetti-Cecchi and Cinelli 1997), testing for interactions between cage effects and grazer removal treatments would require the manipulation of grazer densities independently of the use of cages, which is not feasible. Therefore, these uncaged control plots were designed to test for the direct (e.g. shading and disruption of water flow) and indirect (e.g. altered grazer behaviour) effects of cages on algal assemblages in the presence of ambient grazer densities only, by comparing controls with non-removal caged plots. This approach follows previous studies that have demonstrated no consequences of identical cages on the structure of macroalgal assemblages in mussel beds and rock pools on similar shores (O'Connor and Crowe 2005, O'Connor and Donohue 2013).

The experiment ran for 15 months starting in July 2011 and plots were surveyed at the beginning of the experiment, after three months (October 2011) and after 15 months (October 2012). At each census, percent cover of macroalgal and sessile invertebrate species in each plot was recorded by identifying species under 64 intersections of a  $25 \times 25$  cm quadrat. Species present within the quadrat but not located under an intersection were recorded and assigned a value of 1% each. The quadrat was positioned centrally within plots to avoid edge effects. Total percent cover values often exceeded 100% owing to the multi-layered nature of macroalgal communities. The numbers of grazer species within each plot were also recorded. Treatments were maintained during monthly visits, at which times cages were also cleaned of fouling species or debris to minimise cage effects on assemblages.

To determine whether percent cover served as a reliable proxy for macroalgal biomass, on the final sampling date, a destructive sample of the central  $25 \times 25$  cm area in each experimental

plot was taken to estimate biomass of each macroalgal species (excluding crustose corallines) following drying to constant mass at 60°C. Dry biomass values for *Corallina officinalis* were multiplied by 0.2 to convert them to calcium carbonate-free estimates (Griffin et al. 2010). There was a significant linear relationship between total dry biomass and total cover of macroalgae (excluding crustose corallines), which differed between mussel beds and rock pools (mussel beds:  $\text{biomass [g m}^{-2}] = -2.07 + 4.42 \times \text{cover [\%]}$ ,  $R^2 = 0.929$ ,  $P < 0.001$ ; rock pools:  $\text{biomass} = -31.98 + 1.74 \times \text{cover}$ ,  $R^2 = 0.808$ ,  $P < 0.001$ ).

#### *Data analysis*

For each sampling date separately, differences in macroalgal total cover, taxon richness (S) and evenness (Simpson's  $1-\lambda$ ) were tested using two-way factorial ANOVA involving habitat (fixed, 2 levels) and grazer removal treatment (fixed, 5 levels). Richness and evenness are complementary measures that are recommended for use in studies examining the consequences of biodiversity change (Altieri et al. 2009). Total algal cover was found to differ among grazer removal treatments across both habitats at the start of the experiment, although it was not possible to resolve these differences fully (Supplementary material Appendix 1 Table A1). Therefore, algal cover data were converted into the overall change in total cover to simplify interpretation. We used a priori planned contrasts to test for differences between the single-removal treatments and the multi-removal treatment but, given the limitations on making inferences regarding limpet identity, the variance explained by grazer removal was not partitioned further to isolate grazer 'identity' effects explicitly (Duffy et al. 2005). To test for cage effects, comparisons between caged non-removal plots and uncaged control plots were made for all variables. Prior to ANOVA, Shapiro-Wilk and Cochran's tests were used to check normality and homoscedasticity of data, respectively. In the case of total

cover data for three months, transformation was unable to stabilise heterogeneous variances, therefore results were interpreted with caution by reducing the limit for statistical significance ( $\alpha = 0.01$ ). Student-Newman-Keuls (SNK) tests were used to make post hoc comparisons between levels of significant effects. Although SNK tests have the potential for excessive Type I error rates when treatments fall into groups spaced widely apart (Day and Quinn 1989), which was generally not the case in the current study, a greater problem is the loss of power resulting from the use of alternative procedures where SNK tests would otherwise be suitable (Underwood 1997). Therefore, in this study, SNK tests were an appropriate means of examining alternatives following the rejection of null hypotheses.

Permutational multivariate analysis of variance (PERMANOVA; McArdle and Anderson 2001, Anderson 2001) was used to test for effects of grazer treatments on macroalgal assemblage structure in mussel beds and rock pools, separately for each sampling date, based on the same model structure as the ANOVAs. Analyses were performed on zero-adjusted Bray-Curtis dissimilarity matrices, i.e. via the addition of a dummy species with 1% cover to all plots (Clarke et al. 2006), to deal with instances where no algae were recorded within plots. Tests involved 9,999 permutations of residuals under the reduced model (Anderson and ter Braak 2003). Differences among levels of significant factors were examined with post hoc pairwise permutational *t*-tests. Where significant differences were found, similarity of percentages analysis (SIMPER; Clarke 1993) was used to identify the algal taxa responsible for differences in assemblage structure between treatment levels. To visualise differences in macroalgal assemblage structure among treatment groups, nonmetric multidimensional scaling (MDS) plots were produced. For all multivariate analyses, percent cover data were  $\log_{10}(x+1)$ -transformed to reduce the influence of dominant algal species (Clarke and Warwick 2001). All analyses were conducted in R (v3.0.1; R Development Core Team 2013),

except for the PERMANOVAs, which were performed using the PERMANOVA+ add-on (v1.0.3) in PRIMER (v6.1.13; PRIMER-E Ltd., Plymouth, UK).

## Results

At the start of the experiment, macroalgal total cover, richness and evenness were greater in rock pools than in mussel beds, and macroalgal assemblage structure differed between the two habitats (Appendix 1 Table A1). After three months, there were still differences in algal richness, evenness and assemblage structure between habitats (Fig. 1c,e; Table 1b–d).

Additionally, richness and evenness differed among grazer removal treatments, independently of habitat (Fig. 1c,e; Table 1b,c). Across both mussel beds and rock pools, algal richness was greater in the multi-removal treatment than in any other treatment (Fig. 1c). Although post hoc tests were unable to resolve differences among the non-removal and single-removal treatments fully, the removal of *Patella* appeared to result in an increase in algal richness relative to the non-removal treatment across both habitats (Fig. 1c). Further, algal richness was greater in the multi-removal treatment compared to the single-removal treatments (Table 1b). There also appeared to be an increase in algal evenness in the multi-removal treatment compared to both the non-removal treatment and the *Littorina* single-removal treatment, but post hoc tests were unable to resolve treatment differences fully (Fig. 1e).

After 15 months, the overall decline in total macroalgal cover was greater in rock pools than in mussel beds (Fig. 1b; Table 1a). Again, macroalgal richness and evenness were found to be greater in rock pools compared to mussel beds (Fig. 1d,f; Table 1b,c) and assemblage structure differed between the two habitats (Table 1d). In addition to algal richness, total cover change and assemblage structure were affected by grazer removal independently of



habitat (Fig. 1b,d; Table 1a,b,d). The removal of *Patella* led to an increase in algal richness relative to the non-removal treatment and the other two single-removal treatments (Fig. 1d). Further, the multi-removal of all three grazers resulted in greater algal richness than any other treatment (Fig. 1d) in addition to the mean of the single-removal treatments (Table 1b). The multi-removal treatment led to an overall increase in total algal cover, which appeared to differ significantly from the overall declines exhibited by the non-removal and the *Patella* and *Gibbula* single-removal treatments, but post hoc tests were unable to resolve differences among all treatments fully (Fig. 1b). In terms of algal evenness, there was no longer any effect of grazer removal (Fig. 1f; Table 1c). The presence of cages reduced macroalgal richness at three months (ANOVA;  $F_{1,12} = 5.83$ ,  $P = 0.033$ ; Fig. 1c) and evenness at 15 months ( $F_{1,12} = 5.23$ ,  $P = 0.041$ ; Fig. 1f; Appendix 2 Table A2).

There was a significant interaction between habitat and grazer removal treatments affecting algal assemblage structure after three months, indicating that the responses of algal assemblages to grazer removal differed between mussel beds and rock pools (Fig. 2a,c; Table 1d). Although post hoc tests were unable to resolve differences among treatments fully, they suggested tentatively that, in mussel beds, the *Patella* single-removal and multi-removal treatments resulted in a shift in algal assemblage structure relative to the *Littorina* and *Gibbula* single-removal treatments (Fig. 2a; Appendix 3 Table A3). In contrast, in rock pools, algal assemblage structure appeared to differ only between the non-removal and multi-removal treatments (Fig. 2c; Appendix 3 Table A3). Algal assemblage structure also differed between caged non-removal and uncaged control plots (Appendix 2 Table A2). After 15 months, there was no longer any interactive effect of habitat and grazer removal on algal assemblage structure, indicating that the effects of grazer species loss were consistent between mussel beds and rock pools (Fig. 2b,d; Table 1d). Across both habitats, there was a shift in

algal assemblage structure in the *Patella* single-removal and multi-removal treatments relative to all other treatments (Appendix 3 Table A3). This shift was driven consistently (i.e.  $\bar{\delta}_i/\text{SD}(\delta_i) > 1$ ) by a relative increase in *Fucus vesiculosus* ( $\bar{\delta}_i = 13.3\%$ ) and by relative decreases in calcareous encrusting algae and *Corallina officinalis*, both of which were primarily constituents of rock pool assemblages (Table 2). These changes were accompanied by an increase in *Cladophora rupestris* and fucoid germlings across both habitats (Table 2).

## Discussion

To advance our understanding of the consequences of species loss in the face of changing environmental conditions, we must assess the relative contribution of biodiversity to ecosystem processes across a range of contexts, while incorporating the complexity that characterises natural ecosystems (Duffy et al. 2007, Cardinale et al. 2012). We performed single and multiple removals of common grazer species, or groups of species, simultaneously in mussel beds and rock pools, which represent two contrasting ecological contexts against a background of natural environmental variability. The most striking aspect of our findings is the overall consistency of responses to consumer loss across habitats over the duration of the study, demonstrated by a general lack of interactions between habitat and grazer removal treatments. While the effects of limpet removal cannot be attributed to individual species, the loss of this group of putative key grazers, versus that of other grazer species, resulted in similar relative changes to algal assemblages in mussel beds and rock pools. The fact that this pattern emerged despite obvious differences in grazer densities and relative abundances between habitats, in addition to initial differences in algal assemblages and environmental conditions, suggests that consumer diversity (i.e. both identity and richness) is a major driver of ecological processes in this system. In addition, the changes in the patterns of algal

abundance and diversity over the course of the experiment and the transient habitat-dependent response of algal assemblage structure emphasise that experimental duration is critical to the interpretation of studies examining the effects of species loss across environmental contexts (Cardinale et al. 2004, O'Connor and Crowe 2005, Stachowicz et al. 2008).

In both mussel beds and rock pools, algal total cover, species richness and evenness underwent significant changes in response to grazer removal. In particular, the removal of limpets led to a greater increase in algal richness than the removal of either *Littorina littorea* or *Gibbula umbilicalis*. The key ecological role of patellid limpets, relative to other grazer species, regulating the establishment of algae on emergent substrata and in tide pools on European rocky shores is well known (Hawkins and Hartnoll 1983, O'Connor and Crowe 2005, Coleman et al. 2006, Griffin et al. 2010). The extent of their influence on algal community dynamics in mussel beds, however, is perhaps less well appreciated (O'Connor and Crowe 2008, Crowe et al. 2011). Our findings suggest that the relative functional roles of limpets collectively, whether represented predominantly by *Patella ulyssiponensis* or by *P. vulgata*, may be of similar importance in mussel beds compared to other habitats on rocky shores, in spite of natural differences in total abundance.

Further, the differences among single-removal treatments suggest that other common grazer species, even those present at higher natural densities, appear to be limited in their capacity to compensate for the loss of limpets in mussel beds as well as rock pools (O'Connor and Crowe 2005, Griffin et al. 2010). Although our experiment allowed only for behavioural rather than numerical compensation, previous research has demonstrated that even corresponding increases in the abundance of *L. littorea* and *G. umbilicalis* are insufficient to compensate for limpet removal in this system over similar timescales (O'Connor and Crowe 2005). While we

cannot separate the effects of different limpet species, our results imply some degree of functional complementarity between *P. ulyssiponensis* and *P. vulgata* at the scale of this study owing to their spatial segregation between mussel beds and rock pools (Firth and Crowe 2010). Nonetheless, further experimentation is required to determine precisely how the relative roles of these key species vary across habitats in which they coexist, particularly because other closely related limpet species are known to have idiosyncratic effects on rocky shore communities in this region (Moore et al. 2007).

A key finding of our study was that the removal of multiple grazer species led to a greater increase in algal richness than did the removal of limpets alone, even though the single removal of either *Littorina littorea* or *Gibbula umbilicalis* had no effect. This effect was accompanied by a shift in algal assemblage structure in the limpet single-removal and multi-removal treatments compared to all other treatments, which was driven largely by the increased establishment and growth of fucoid macroalgae at the apparent expense of other species. While consumer identity can be of overarching importance for the functioning of marine ecosystems (O'Connor and Crowe 2005, Stachowicz et al. 2007), declines in consumer diversity per se may lead to reduced top-down control owing to trait differentiation among consumer species in terms of, for example, feeding preferences (Duffy 2002, Griffin et al. 2009).

Alternatively, these patterns may have resulted from the reduction in grazer abundance associated with the multi-removal treatment in our 'subtractive' experimental design, rather than a reduction in grazer species richness. For example, the establishment of fucoid macroalgae on rocky shores may occur only when grazer density falls below a certain threshold (Jonsson et al. 2006). Indeed, the effects of grazer removal observed here may have

415 been driven, at least in part, by differences in density among experimental treatments as  
416 opposed to grazer identity or richness. Previous research has emphasised the importance of  
417 density-dependent effects in regulating biodiversity–ecosystem functioning relationships (e.g.  
418 Benedetti-Cecchi 2004, Maggi et al. 2009). To improve our understanding of complex, non-  
419 linear effects of consumer species loss, future studies should aim to separate the importance  
420 of consumer density from that of identity and richness, such as by incorporating density  
421 explicitly as an additional treatment (Benedetti-Cecchi 2004, Byrnes and Stachowicz 2009).  
422 While there were logistical constraints on the maximum number of treatments and replicates  
423 in our study, incorporating (rather than eliminating) differences in grazer density between  
424 treatments helped to maintain the relevance of our findings to species loss from natural  
425 habitats in this system, at least for comparable spatial and temporal scales. Importantly, even  
426 though the mechanisms underlying differences between the single-removal and multi-removal  
427 treatments are unclear, our results suggest that, in both mussel beds and rock pools, the roles  
428 of grazer species, or groups of species, depend on the presence or absence of other grazers  
429 and, therefore, cannot be deduced from the effects of their removal in isolation.

430  
431 Initially, grazer-driven changes in algal assemblage structure varied according to habitat.  
432 Although the mechanisms driving this context-dependency remain unclear, there was some  
433 indication of a greater overall response of algal assemblages, at least in terms of the number  
434 of differences between treatment groups, in mussel beds compared to rock pools.  
435 Nonetheless, the suggestion of a transient effect of habitat on community responses highlights  
436 the importance of experimental duration in assessing the consequences of species loss from  
437 complex ecosystems (O'Connor and Crowe 2005, Stachowicz et al. 2008). It is perhaps  
438 surprising that habitat-dependent effects of grazer removal were not more common in our  
439 study, given the contrasting patterns of environmental heterogeneity (Metaxas and Scheibling

1993) and inherent differences in the abundance and structure of grazer and algal assemblages between habitats (e.g. the difference in limpet densities between mussel beds and rock pools). Instead, for the majority of responses measured in our study, the effects of grazer removal on algal assemblages were remarkably consistent across habitats. Although this may mean that the effects of consumer loss on algal communities were not mediated strongly by local-scale variability between habitats on the same shore, other processes such as variation in recruitment or disturbance regimes may play a greater role over larger scales (Jenkins et al. 2005, Mrowicki et al. 2014). For example, divergent effects of grazer removal may emerge even in similar habitats on different rocky shores separated by kilometres (Crowe et al. 2011). While the consequences of changing diversity are expected to be more apparent over larger spatial and temporal scales (Cardinale et al. 2004, Stachowicz et al. 2008), it is less clear how the importance of abiotic factors in determining the effects of species loss varies across multiple scales.

There are some caveats that should be considered when attempting to extend our findings to rocky intertidal systems in general. First, the presence of experimental cages appeared to influence the structure of algal assemblages, either directly, via shading or hydrodynamic disruption, or indirectly, by altering the movement of grazers or providing habitat for other consumers. Owing to the nature of the study system, cages were the most suitable means of manipulating grazer populations over the timescale of the experiment, and it was not possible to test whether cage effects interacted with grazer removal treatment. The fact that clear differences emerged among caged treatments despite substantial environmental variability within and between habitats, however, suggests that the observed effects of grazer species loss may indeed be representative of unmanipulated, 'real world' communities within this system. Second, it was found that total algal cover was not equivalent across treatments at the

start of the experiment, which may have influenced the responses of algal assemblages to grazer removal. The initial pattern of algal cover, however, did not correspond with that observed later in the experiment, in addition to the differences (or lack thereof) in richness and evenness between treatments. Again, this suggests that grazer removal was the most important force driving changes in algal assemblages over the course of the experiment. While it is important to exercise caution in relating the results of manipulative studies to real world scenarios, field-based removal experiments are useful for understanding how complex ecosystems respond to species loss, serving as much-needed tests of fundamental ecological theory (Díaz et al. 2003, Stachowicz et al. 2008, Gamfeldt et al. in press).

In conclusion, our results demonstrate that the relative effects of the loss of key groups of consumers can transcend different physical and biological conditions between habitats. Specifically, limpets, which comprised predominantly *Patella vulgata* in mussel beds and *P. ulyssiponensis* in rock pools, were of comparable importance, in relation to *Littorina littorea* and *Gibbula umbilicalis*, in the maintenance of the abundance, diversity and structure of algal assemblages. We found clear effects of grazer removal despite inherent environmental heterogeneity both between and within habitats, which provides compelling evidence of the overarching importance of these grazer species across the contexts examined in this study. On European rocky shores, community processes and energy transfer are driven by the spatial and temporal dynamics of algae, which in turn are regulated largely by the activities of such mobile grazers (Hawkins and Hartnoll 1983). Therefore, although the applicability of our findings to other rocky shore habitats remains to be tested, shifts in the dynamics of algal communities resulting from changing compositions and densities of consumer populations may have important consequences across multiple environmental contexts in coastal ecosystems. Overall, while it is clear that biodiversity plays a fundamental role in driving

ecosystem functioning, our ability to predict the ecological consequences of species loss will be enhanced by determining the range of relevant contexts and scales over which it has the greatest influence, particularly against the current background of global environmental change (Hooper et al. 2012).

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621 Supplementary material (Appendix oik.XXXX at  
622 <[www.oikosjournal.org/readers/appendix](http://www.oikosjournal.org/readers/appendix)>). Appendix 1–3.

623 **Tables**

624 **Table 1.** ANOVAs and PERMANOVA testing effects of habitat (mussel beds versus rock pools) and grazer removal treatments (non-removal;  
 625 single-removals of *Patella*, *Littorina* and *Gibbula*; multi-removal of all three grazers) on macroalgal (a) total cover change, (b) taxonomic  
 626 richness, (c) Simpson's evenness ( $1-\lambda$ ) and (d) assemblage structure, after three and 15 months. Initial total algal cover and grazer density are  
 627 included as covariates. Significant *P*-values are highlighted in bold.

Source of variation	DF	(a) Total cover change <sup>†</sup>			(b) Richness			(c) Evenness			(d) Assemblage structure		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	Pseudo- <i>F</i>	<i>P</i>
Three months:													
Habitat, H	1	23.93	0.07	0.789	455.62	236.69	<0.001	0.62	13.13	0.001	64400.00	93.74	<0.001
Grazer removal, Gr	4	479.77	1.46	0.240	19.29	10.02	<0.001	0.16	3.41	0.021	2155.10	3.14	<0.001
Single vs. multi	1	802.15	2.43	0.129	37.50	19.48	<0.001	0.18	3.78	0.061	3086.90	3.91	0.006
H × Gr	4	62.87	0.19	0.941	3.81	1.98	0.123	0.06	1.29	0.295	1771.70	2.58	<0.001
Residual	30	329.59			1.92			0.05			686.99		
15 months:													
H	1	1329.00	6.13	0.019	250.00	100.00	<0.001	0.20	5.45	0.026	56223.00	75.95	<0.001
Gr	4	1510.80	6.96	<0.001	37.96	15.19	<0.001	0.09	2.60	0.056	3770.90	5.09	<0.001
Single vs. multi	1	3711.80	17.11	<0.001	82.51	33.00	<0.001	0.12	3.42	0.074	7052.70	7.74	<0.001
H × Gr	4	199.60	0.92	0.465	0.69	0.28	0.892	0.02	0.63	0.644	1090.10	1.47	0.089
Residual	30	216.90			2.50			0.04			740.24		

628 <sup>†</sup>Transformation of data for three months was unable to stabilise heterogeneous variances.

**Table 2.** SIMPER analysis of algal assemblage structure across both habitats (mussel beds and rock pools) after 15 months, comparing the treatments involving the removal of *Patella* (the *Patella* single-removal treatment and the multi-removal treatment) to all other grazer removal treatments collectively (the non-removal treatment and the *Littorina* and *Gibbula* single-removal treatments).  $\bar{\delta}_i/SD(\delta_i)$  = average species contribution to group dissimilarity divided by standard deviation of contributions;  $\bar{\delta}_i\%$  = percent contribution of species to overall between-group dissimilarity. Calculations are based on  $\log_{10}(x+1)$ -transformed species abundances. Only the most important species ( $\bar{\delta}_i > 3\%$ ) are shown.

Species	Mean cover (%)		$\bar{\delta}_i/SD(\delta_i)$	$\bar{\delta}_i\%$
	<i>Patella</i> and			
	multi-removal treatments	Other removal treatments		
<i>Fucus vesiculosus</i>	11.91	0.50	1.50	13.32
<i>Lithothamnion</i> spp.	18.62	27.60	1.04	12.69
<i>Corallina officinalis</i> <sup>†</sup>	30.66	19.79	1.08	12.59
<i>F. spiralis</i>	6.15	0.07	0.87	8.82
<i>Ceramium shuttleworthianum</i> <sup>‡</sup>	1.37	2.17	0.86	6.97
<i>Gelidium pusillum</i>	2.37	1.44	0.98	5.44
<i>Cladophora rupestris</i>	2.37	1.58	1.15	5.18
<i>Fucus</i> sp. (juvenile)	0.95	0.04	1.05	4.51
<i>Asparagopsis armata</i> <sup>†</sup>	0.58	1.84	0.90	3.73
<i>Ulva intestinalis</i> <sup>‡</sup>	0.88	0.13	0.55	3.39
<i>Polysiphonia fucoides</i> <sup>†</sup>	0.94	1.45	0.86	3.30

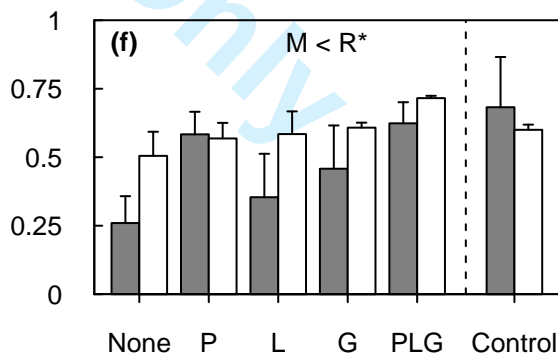
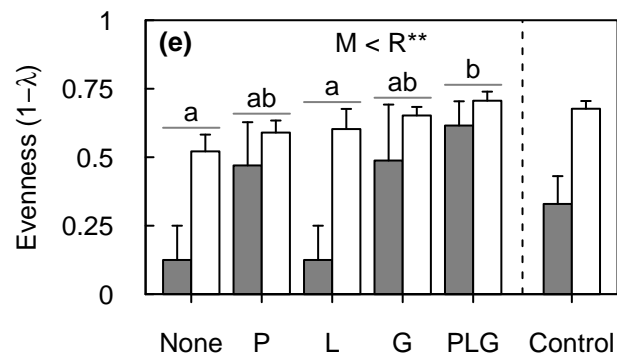
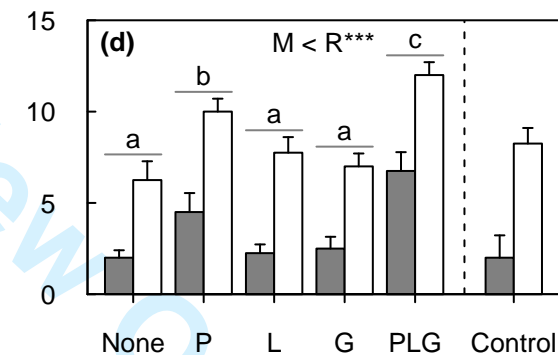
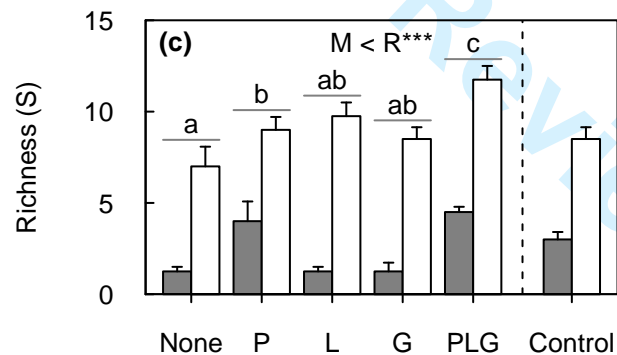
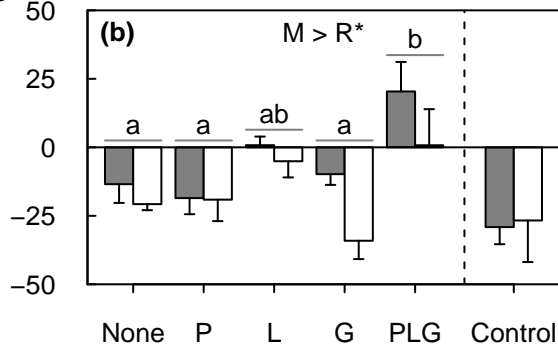
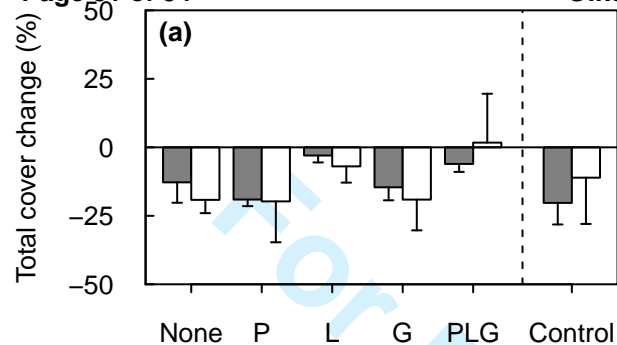
<sup>†</sup>Recorded in rock pools only; <sup>‡</sup>Recorded in mussel beds only.

## Figure legends

**Figure 1.** Mean (+ or – SE) macroalgal (a,b) total cover change, (c,d) species richness and (e,f) evenness for different grazer removal treatments (None = non-removal; P, L and G = single-removal of *Patella*, *Littorina* and *Gibbula*, respectively; PLG = multi-removal of all three grazers) in mussel beds (shaded bars, M) and rock pools (open bars, R), after (a,c,e) three and (b,d,f) 15 months. ‘M  $\neq$  R’ indicates a significant difference between habitats (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ), based on ANOVA results. Letters denote grazer removal groups (i.e. across both levels of habitat) that are not significantly different ( $P \geq 0.05$ ), based on post hoc SNK tests, to illustrate significant main effects of grazer removal independently of habitat.

**Figure 2.** Non-metric MDS ordinations of macroalgal assemblages for different grazer removal treatments (None = non-removal; P, L and G = single-removal of *Patella*, *Littorina* and *Gibbula*, respectively; PLG = multi-removal of all three grazers) in (a,b) mussel beds and (c,d) rock pools after (a,c) three and (b,d) 15 months, based on  $\log_{10}(x+1)$ -transformed species abundances. Care should be taken when interpreting plots for which stress  $> 0.2$  (Clarke 1993).





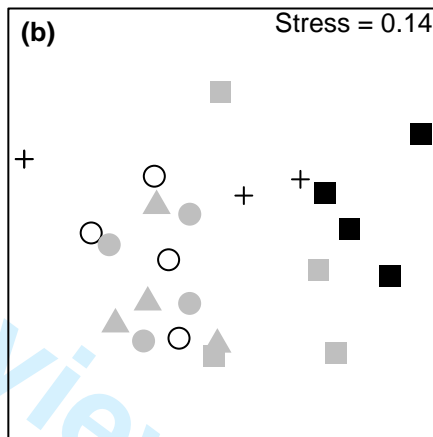
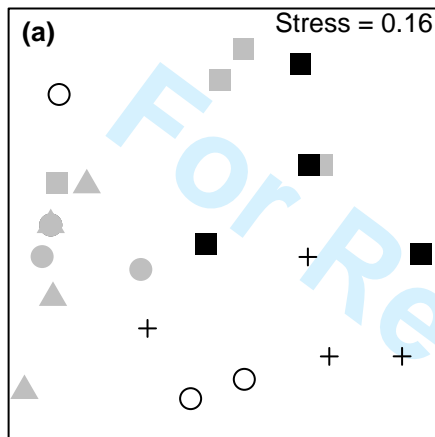
Grazers removed

Grazers removed

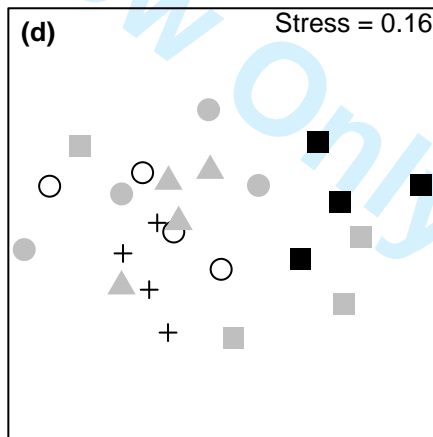
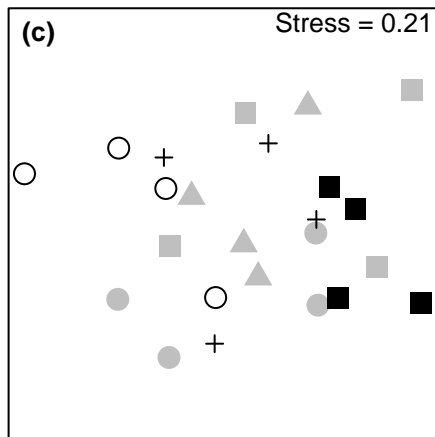
Species removed

- None
- P
- L
- ▲ G
- PLG
- + Control

Mussel beds



Rock pools



CONSISTENT EFFECTS OF CONSUMER SPECIES LOSS ACROSS DIFFERENT HABITATS

ROBERT J. MROWICKI, CHRISTINE A. MAGGS & NESSA E. O’CONNOR

**Appendix 1.** Results of tests for differences in algal assemblages among treatments at the start of the experiment.

**Table A1.** ANOVAs and PERMANOVA testing effects of habitat (mussel beds versus rock pools) and grazer removal treatments (non-removal; single-removals of *Patella*, *Littorina* and *Gibbula*; multi-removal of all three grazers) on macroalgal (a) total cover, (b) taxonomic richness, (c) Simpson’s evenness ( $1-\lambda$ ) and (d) assemblage structure at the start of the experiment in July 2011. Significant *P*-values are highlighted in bold.

Source of variation	DF	(a) Total cover			(b) Richness			(c) Evenness <sup>†</sup>			(d) Assemblage structure		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	Pseudo- <i>F</i>	<i>P</i>
Habitat, H	1	156622.00	615.84	<0.001	161.33	80.67	<0.001	0.60	20.38	<0.001	69095.00	76.70	<0.001
Grazer removal, Gr	5	816.00	3.21	0.017 <sup>*</sup>	4.88	2.44	0.053	0.05	1.54	0.201	1407.00	1.56	0.073
H × Gr	5	294.00	1.16	0.350	2.43	1.22	0.321	0.02	0.70	0.630	1307.30	1.45	0.114
Residual	36	254.00			2.00			0.03			900.85		

<sup>†</sup>Data were squared to improve normality and stabilise heterogeneous variances; <sup>\*</sup>Student-Newman-Keuls post hoc tests were unable to resolve differences fully among grazer removal treatments.

## CONSISTENT EFFECTS OF CONSUMER SPECIES LOSS ACROSS DIFFERENT HABITATS

ROBERT J. MROWICKI, CHRISTINE A. MAGGS & NESSA E. O'CONNOR

**Appendix 2.** Results of tests for the effects of experimental cages on algal assemblages.

**Table A2.** ANOVAs and PERMANOVA testing the effects of habitat (mussel beds versus rock pools) and the presence of cages (caged non-removal treatment versus uncaged control treatment) on macroalgal (a) total cover change, (b) taxonomic richness, (c) Simpson's evenness ( $1-\lambda$ ) and (d) assemblage structure, after three (October 2011) and 15 (October 2012) months. Significant *P*-values are highlighted in bold.

Source of variation	DF	(a) Total cover change <sup>†</sup>			(b) Richness			(c) Evenness <sup>‡</sup>			(d) Assemblage structure		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	Pseudo- <i>F</i>	<i>P</i>
Three months:													
Habitat, H	1	7.91	0.02	0.894	126.56	69.83	<0.001	0.29	18.57	0.001	26479.00	30.47	<0.001
Cage, C	1	0.35	0.00	0.978	10.56	5.83	0.033	0.06	4.10	0.066	2541.60	2.92	0.029
H × C	1	243.17	0.57	0.465	0.06	0.03	0.856	0.01	0.64	0.439	1807.90	2.08	0.096
Residual	12	426.59			1.81			0.02			869.07		
15 months:													
H	1	2 × 10 <sup>-4</sup>	3 × 10 <sup>-3</sup>	0.959	110.25	31.88	<0.001	0.03	0.52	0.486	25273.00	28.18	<0.001
C	1	0.05	0.74	0.408	4.00	1.16	0.303	0.27	5.23	0.041	1046.60	1.17	0.310
H × C	1	0.08	1.21	0.292	4.00	1.16	0.303	0.11	2.09	0.174	1183.70	1.32	0.254
Residual	12	0.07			3.46			0.05			896.76		

<sup>†</sup>Data for 15 months were squared to stabilise heterogeneous variances; <sup>‡</sup>Data for three months were squared to improve non-normality.

CONSISTENT EFFECTS OF CONSUMER SPECIES LOSS ACROSS  
DIFFERENT HABITATS

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**Appendix 3.** Results of post hoc tests for differences in algal assemblage structure among experimental treatments.

**Table A3.** PERMANOVA post hoc pairwise tests of differences in algal assemblage structure among grazer removal treatments (None = non-removal; P, L and G = single-removal of *Patella*, *Littorina* and *Gibbula*, respectively; PLG = multi-removal of all three grazers), (a) after three months, for mussel beds and rock pools separately, and (b) 15 months, across both habitats. Significant *P*-values are highlighted in bold.

Comparison	(a) Three months <sup>†</sup>				(b) 15 months	
	Mussel beds		Rock pools		Both habitats	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
None vs. P	1.38	0.161	1.31	0.178	1.88	<b>0.012</b>
None vs. L	1.07	0.339	1.48	0.100	1.14	0.280
None vs. G	1.08	0.337	1.36	0.152	0.88	0.555
None vs. PLG	1.59	0.099	2.44	<b>0.011</b>	3.38	<b>&lt;0.001</b>
P vs. L	2.47	<b>0.016</b>	1.31	0.180	2.27	<b>0.003</b>
P vs. G	2.14	<b>0.022</b>	0.97	0.443	2.00	<b>0.009</b>
P vs. PLG	1.18	0.272	1.31	0.176	1.49	0.054
L vs. G	0.68	0.686	1.21	0.233	1.03	0.407
L vs. PLG	2.98	<b>0.007</b>	1.17	0.273	3.37	<b>&lt;0.001</b>
G vs. PLG	2.34	<b>0.012</b>	1.54	0.078	3.41	<b>0.001</b>

<sup>†</sup>Owing to the low number of possible permutations ( $\leq 35$ ), Monte Carlo asymptotic *P*-values, rather than standard permutational *P*-values, are presented.